

## Skeletal Anatomy of the Mesosoma of *Palaeomyrmex anomalus* (Blood & Kryger, 1922) (Hymenoptera: Mymarommatidae)

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*Abstract.*—Detailed study of the skeletal anatomy of the mesosoma of *Palaeomyrmex anomalus* was undertaken, primarily with SEM. Four previously unrecognized putative autapomorphies for the Mymarommatidae were discovered: 1) absence of a functional anterior thoracic spiracle; 2) fusion of the propleural arm with the profurcal arm; 3) presence of a pair of rods on the anterior surface of the prothorax; and 4) absence of the metafurca. The presence of a concealed prepectus fused with the posterolateral margin of the pronotum was confirmed. Additional features of possible significance for evaluating the phylogenetic position of Mymarommatidae are described and discussed. A sister-group relationship with the Chalcidoidea is the most well supported hypothesis presently, but needs additional corroboration.

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The small family Mymarommatidae is arguably the most enigmatic wasp taxon. Eight extant and ten extinct species have been described (Grimaldi and Engel 2005). The biology of these minute wasps is almost entirely unknown. They appear to be associated with leaf litter and were reared once from a bracket fungus (Gibson et al. 1999). Because of the small size of the adults (immatures are unknown), it has been suggested that they are egg parasitoids, but this is entirely conjectural. The absence of biological information for Mymarommatidae is all the more intriguing because they display a number of highly unusual autapomorphic features, which in the case of head anatomy border on the bizarre—the occipital region is separated from the remainder of the head capsule by an expanse of pleated membrane that allows the head to expand and contract in an accordion-like manner (see Gibson 1986, fig. 9). Also, the prosternum and propleura are extensively fused, forming a continuous carapace in external view; the mesopleuron is fused along most of its posterior margin

to the metapleuron-propodeum (Gibson 1986, fig. 10); the fore wing has a reticulate pattern on the surface (not to be confused with true wing venation; Gibson 1986, fig. 30); and the hind wing is reduced to a rodlike structure that apically is bifurcate to clasp and support the base of the forewing (Gibson 1986, fig. 33). Further putative autapomorphies are discussed by Gibson (1986) and Gibson et al. (1999) (see also below).

While there has never been any serious doubt about the monophyly of the Mymarommatidae, their phylogenetic position within the Hymenoptera is less well corroborated. Debauche (1948) was the first to place them in their own family (Mymarommatidae [sic]), removing them from Mymaridae. This was reversed by some subsequent authors. The first comprehensive discussion of mymarommatid affinities in a cladistic context was undertaken by Gibson (1986), who placed them as sister group to the Chalcidoidea. The main evidence for this is the presence of axillar phragmata, apodemes projecting

under the mesoscutum and accommodating the origins of the mesotergal-trochanteral muscles (Gibson 1986, 1999, Gibson et al. 1999). This hypothesis was later supported by the phylogenetic analyses of Ronquist et al. (1999).

Debauche (1948) provided an overview of the anatomy of *Palaeomymar anomalum*. Gibson (1986) and Heraty et al. (1994) treated selected aspects of mesosomal anatomy in considerable detail, but a comprehensive survey of this body region in Mymarommatidae is wanting. The present paper examines the external and internal skeletal anatomy of the mesosoma and anterior part of the metasoma (the petiole) for *P. anomalum*. Findings will be discussed in a phylogenetic context, drawing on information obtained from ongoing surveys of the mesosoma in Hymenoptera in general and Chalcidoidea in particular, undertaken by L. Vilhelmsen and L. Krogmann, respectively.

## MATERIALS AND METHODS

*Examined material.*—*Palaeomymar anomalum* (Blood & Kryger, 1922). GERMANY, Niedersachsen, Lüchow-Dannenberg, NSG Forst Lucie. Car net. 15.viii.2001. Leg. H. Meybohm. 5 females. Specimens and vouchers deposited in Zoologisches Museum Hamburg. SWEDEN, Sm[åland], Älmhults kommun, Stenbrohult, Djäkabygds bokbacke, N56°36.548', E14°11.583' (=Trap ID 24). Heath with old beeches. 1.–18.viii.2003 (=coll. event ID 818). Leg. Swedish Malaise Trap Project (Swedish Museum of Natural History). 6 females. Specimens and vouchers deposited in the Zoological Museum, University of Copenhagen.

*Procedure for slide mounting.*—Two specimens were dissected and mounted on a slide in Entellan.

*Procedure for SEM-investigations.*—Specimens were cleaned in a sonicator and dissected with small razor blade scalpels and minutien needles. The preparations were macerated in KOH for a few hours at 40°C or overnight at room temperature,

rinsed in demineralised water and transferred to 70% ethanol. They were then transferred through a series of intermediate concentrations to absolute ethanol, which served as the transition medium for critical point drying. After critical point drying, the preparations were mounted on stubs with double-adhesive tape and coated with platinum prior to examination in a Jeol JSM-6335F field emission SEM unit.

## RESULTS

The mesosoma of *Palaeomymar anomalum* is a compact structure. It can be subdivided into four major components that are comparatively easily separated by dissection (Fig. 1): 1) the pronotum; 2) the propectus, comprising the propleura and prosternum and accommodating the head articulation and foreleg attachments; 3) the mesonotum and attached pro- and mesophragma; 4) the mesopectus-metathorax-propodeum complex. The latter is by far the largest part of the mesosoma and is extensively fused to a degree where the boundaries between the individual parts are not obvious.

In the following, each of these regions are described in turn. In addition, we describe in detail the anterior part of the petiole comprising the mesosoma-metasoma articulation.

*Pronotum.*—Pronotum narrow medially (Fig. 3), laterally expanded into trapezoidal flange (Figs 2, 3); posteriorly articulating with mesopectus, ventrally with propectus (Fig. 1); with sparse, striate sculpture, except for small median band of dense, raised longitudinal striations (Fig. 3); sublaterally with deep dorsal depression posterior to distinct vertical carina extending almost entire height of pronotum (Figs 2, 3). Anteromedian margin in frontal view distinctly incurved (Fig. 3), forming slightly upturned lip just anterior of transverse pronotal sulcus; internally, anteromedian margin inflected, the median part of pronotum with concavity accommodating prophragma (Fig. 5). Dorsal margin in

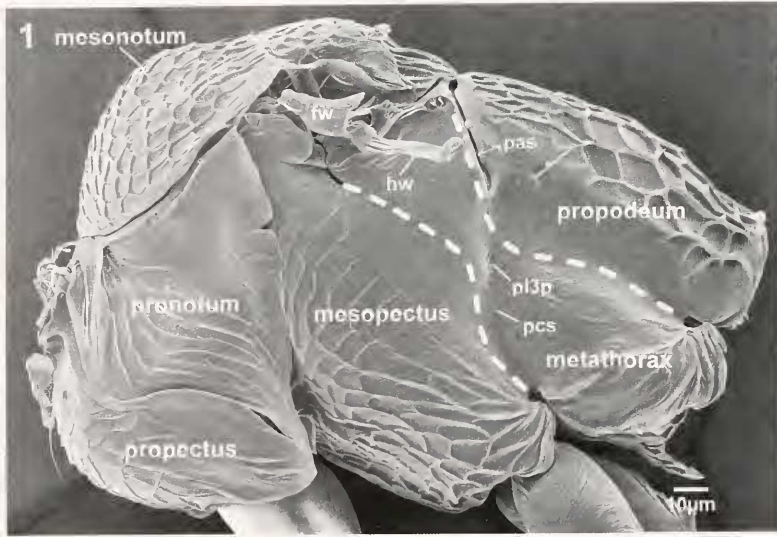


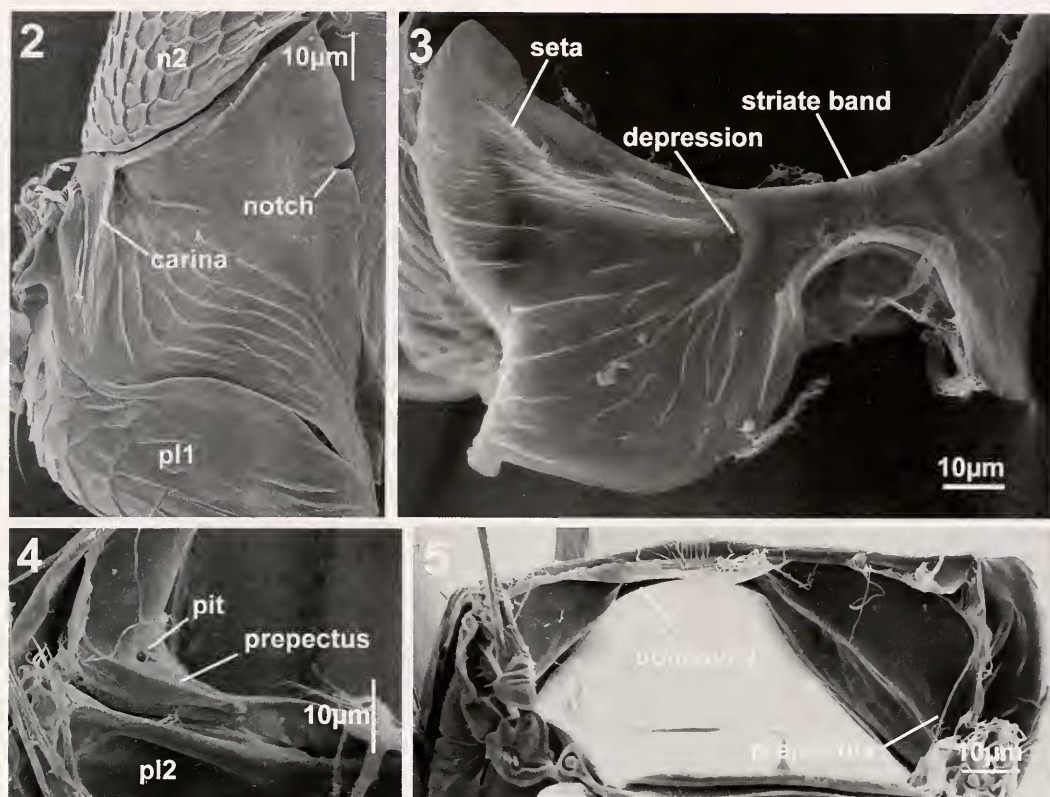
Fig. 1. Lateral view of mesosoma of *Palaeomymar anomalum*. Stippled lines indicate approximate boundaries between mesopectus, metathorax, and propodeum. Abbreviations: fw = fore wing base; hw = hind wing; pas = propodeal antecostal suture; pcs = paracoxal sulcus; pl3p = metapleural pit.

dorsal view deeply incurved, in lateral view with long seta laterally close to dorsal margin (Figs 2, 3). Posterolateral margin almost straight, with small notch about 1/3 of total height from posterodorsal corner (Fig. 2); posteroventral corner extended ventrally between pro- and mesopectus, slender (Fig. 2). Internally, pronotum predominantly smooth, posterolateral margin flanking low vertical carina (Figs 4, 5), the carina (interpreted as the propectus, see discussion) extending for some distance, but neither reaching dorsal nor ventral margin of pronotum, and deflected anteriorly prior to reaching dorsal margin; small pit just anterior of carina (Fig. 4) associated with narrow strands of tissue. Anterior thoracic ('mesothoracic') spiracle not observed internally or externally.

*Propectus*.—Propleural cervical prominence (Fig. 7, cep) with head articulation at anterodorsal corner of propectus, not retracted, separated from rest of propleura by transverse carina (Fig. 7); two short setae situated anteriorly of carina, one posteriorly. Cervical swellings with patch of sensilla, otherwise not developed. Pro-

pleura in ventral view linearly separated anteromedially, fused posteromedially (Figs 6, 7); anteriorly with 1 or 2 elongate setae sublaterally (Fig. 6); posteriorly with carinate margin slightly extended posteromedially (Fig. 6). Propleura laterally with an oblique longitudinal carina separating lateral, dorsal smooth part from ventrally reticulate surface; posterior part of carina laterally delimiting distinct groove accommodating lateroventral margin of pronotum and proximal part of procoxa (Fig. 8). Internally, propleural arm on posterodorsal corner of propleuron slender, projecting posteriorly, posterior end fused with lateral end of profurcal arm (Fig. 9, ppa). Prosternum (Fig. 8, st1) reduced in size, inflected at an angle of about 90 degrees relative to posterior part of propleura and not visible externally (Fig. 6); extensively fused with propleura ventrally, the boundary of fusion indiscernible; externally smooth, expanded dorsally of narrow procoxal cavities, separate from propleura laterally and with slit-like profurcal pit medially (Fig. 8, fu1p). Internally, profurcal base narrow, not extending far anteri-





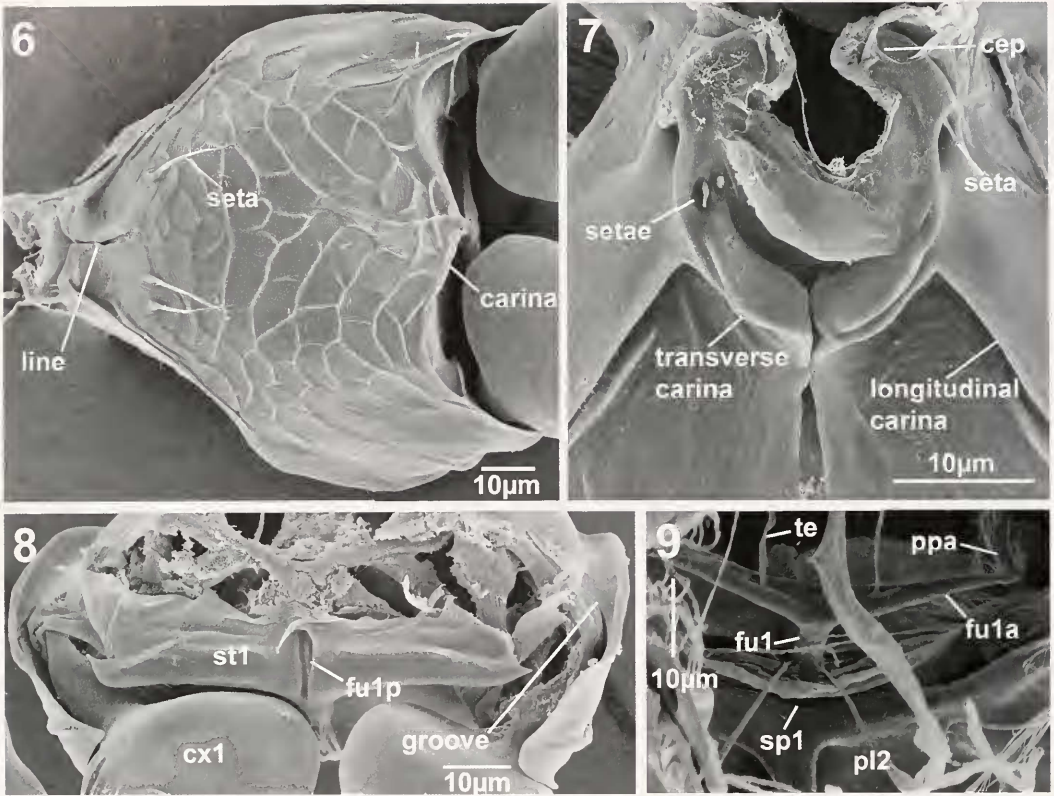
Figs 2–5. Pronotum of *P. anomalum*. 2. Exterior lateral view. 3. Exterior anterior view. 4. Interior view of pronotal-mesopetal junction showing prepectus (dorsal surface to left). 5. Interior, posterior view. Abbreviations: n2 = mesonotum; pl1 = propleuron; pl2 = mesopleuron.

only (Fig. 9, fu1), profurcal arms slender, extending laterally (Fig. 9, fu1a); profurcal bridge absent, anterior profurcal apodemes not developed, only slender tendons present sublaterally (Fig. 9, te). Procoxae very reduced proximally, without transverse carina. Katepisterna and prosternal sclerites not observed.

*Mesonotum*.—Externally, mesonotum predominantly with reticulate sculpture (Fig. 10). Internally, prophragma well developed, projecting anteriorly under pronotum, not subdivided medially nor extended laterally (Figs 12, 14, ph1); dorsal surface of prophragma with paired, anteriorly projecting, slender cylindrical rods submedially, the rods extending at an angle of approx. 90 degrees to each other (Fig. 14) but continuous medially, some-

times with tonofibrillae (Fig. 14, tf) distally and apparently closely associated with dorsomedian margin of pronotum. Mesoscutum with transverse groove just dorsal to rods between its external surface and prophragma accommodating dorsal margin of pronotum. Mesoscutum with median mesoscutal sulcus, notaulus, and parapsidal lines entirely absent externally and internally (Figs 10, 12); with two elongate setae posterolaterally just anterior to transscutal articulation (Fig. 10); transscutal articulation complete, straight (Fig. 10, tsa); parascutal carina well developed laterally, overhanging posterodorsal margin of pronotum and fore wing articulation point (Fig. 16, psc) and extending posterior to lateral end of transscutal articulation (Fig. 10, psc), with two elongate setae

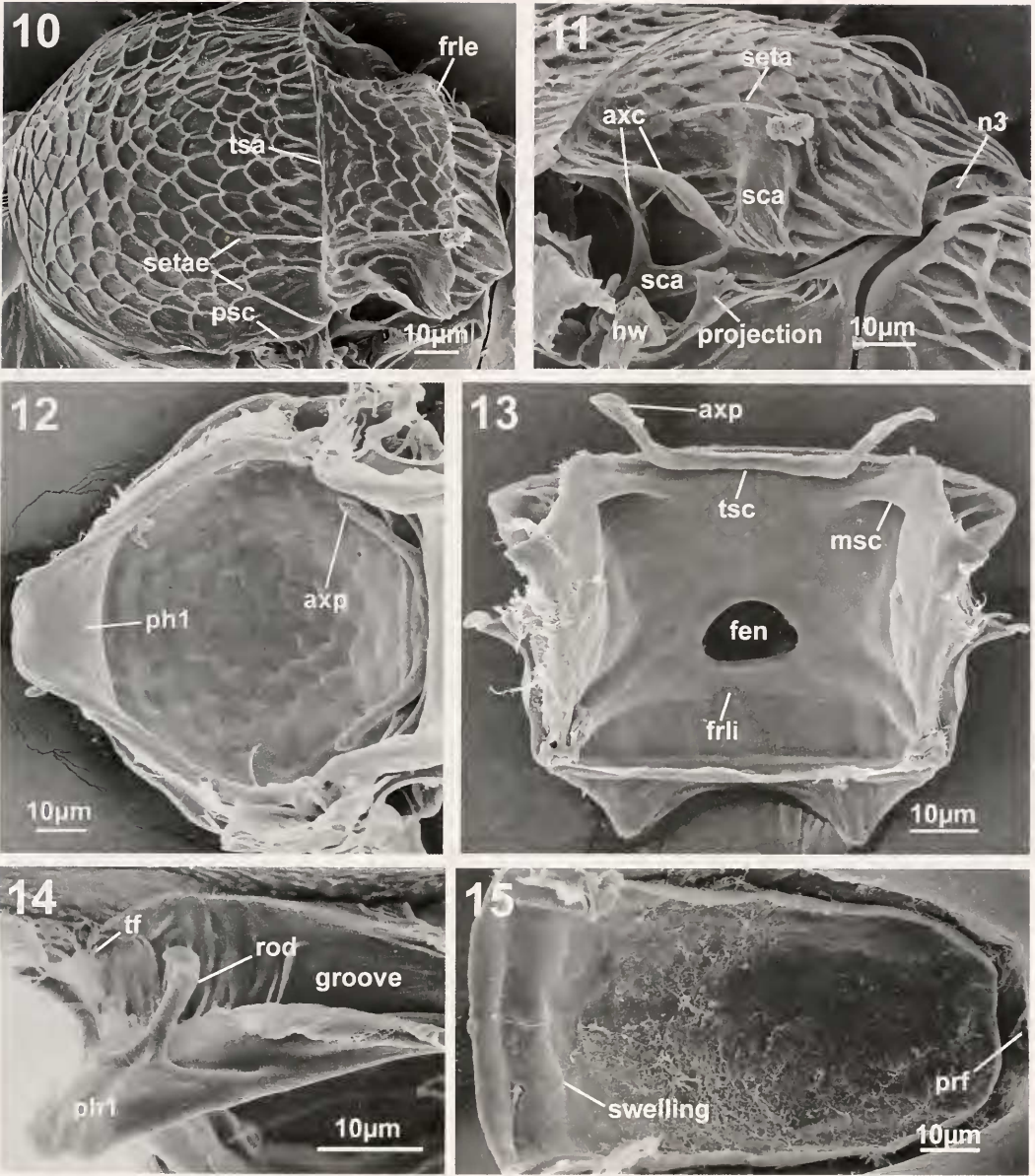




Figs 6–9. Propectus of *P. anomalum*. 6. Exterior ventral view; 7. Exterior anterior view. 8. Prosternum, posterior view (pronotum removed); 9. Profurca, dorsal view. Abbreviations: cep = cervical prominence; cx1 = procoxa; fu1 = profurca; fu1a = profurcal arm; fu1p = profurcal pit; pl2 = mesopleuron; st1 = prosternum; ppa = propleural arm; sp1: prospinasternum; te = tendon.

below parascutal carina just above fore wing base (Fig. 16). Tegula absent. Mesoscutellum with convex, reticulate anteromedian part between lateral depressed areas having more weakly developed sculpture, and with depressed, longitudinally striate posterior frenum (Figs 10, 11) anteriorly delimited by external frenal line (Fig. 10, frle); convex median part with elongate seta laterally, without evident scutoscuteellar sulcus (Figs 10, 11); frenum with sublateral triangular extension overlapping metanotum dorsally (Fig. 11, n3). Mesoscutellum with axillar carina distinct laterally (Figs 11, 16, axc), the carina subdivided posteriorly into posterodorsal branch extending across mesoscutellar arm proximally and anteroventral branch

extending to distal end of mesoscutellar arm (Fig. 11, sca); anteroventral branch of axillar carina with seta. Mesoscutellar arm evident dorsolaterally on mesoscutellum just anterior of frenum (Fig. 11, sca), and with anterolateral part of arm slightly overhanging fore wing base and terminating in slender vertical rod just anteriorly of hind wing base (Fig. 11, hw). Internally, mesoscutellum delimited by low mesoscutellar carina anterolaterally, the carina not continuous medially (Fig. 13, msc); surface spanned by extended septum penetrated by small oval fenestrum in middle (Fig. 13, fen) and with a convex line (Fig. 13, frli) corresponding to external frenal line delimiting oblong transverse impression posteriorly of fenestrum;

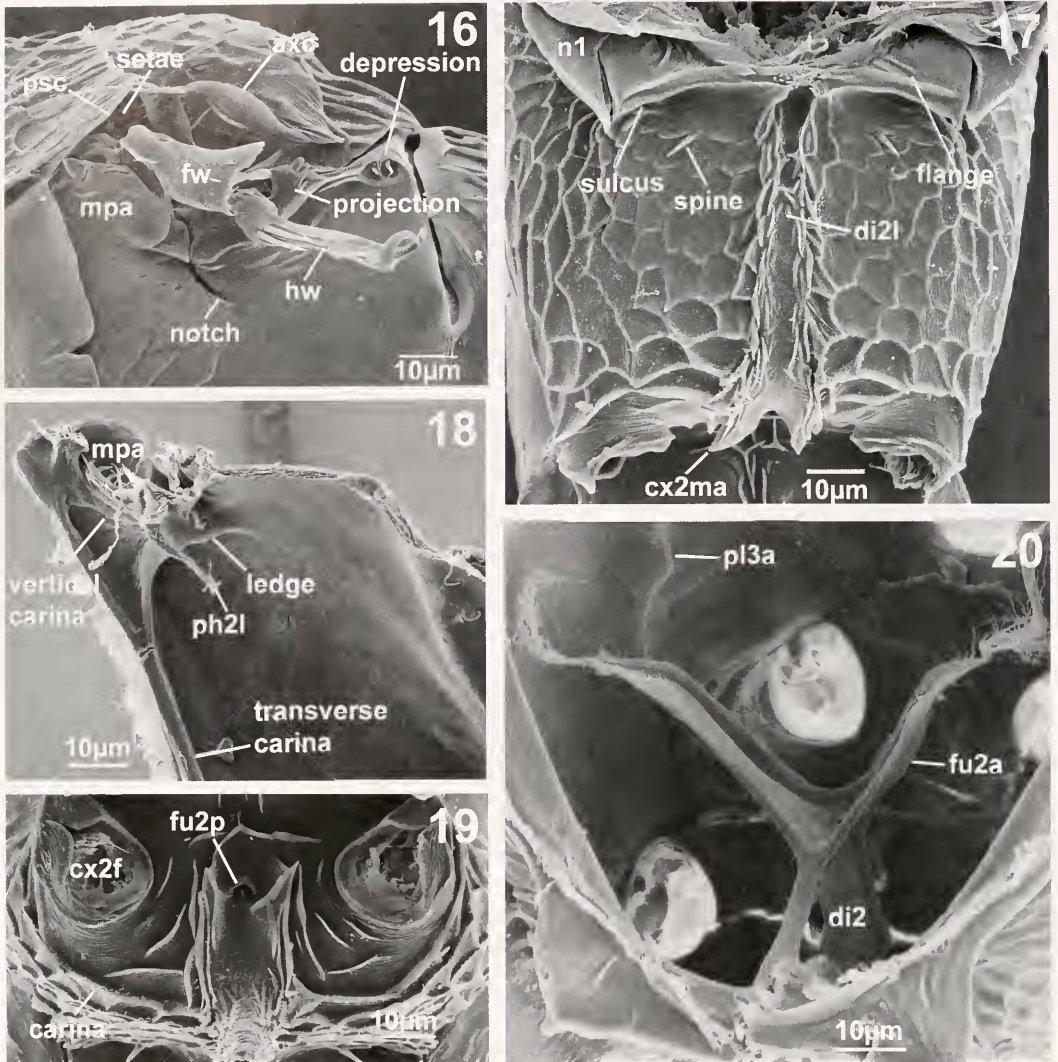


Figs 10–15. Mesonotum of *P. anomalum*. 10. Mesonotum, dorsal view. 11. Mesoscutellum and axilla, posterolateral view. 12. Mesoscutum, ventral view. 13. Mesoscutellum, ventral view. 14. Prothorax, anterolateral view. 15. Mesophragma, ventral view. Abbreviations: axc = axillar carina; axp = axillar phragma; fen = fenestrum; frle = external frenal line; frli = internal frenal line; hw = hind wing; msc = mesoscutellar carina; n3 = metanotum; ph1 = prothorax; prf = propodeal foramen; psc = parascutal carina; sca = mesoscutellar arm; tf = tonofibrillae; tsa = transscutal articulation; tsc = transscutal carina.

anteriorly with rod-like axillar phragmata (Figs 12, 13, axp) arising just posterior of transscutal articulation, the rods continuous medially along transscutal carina

(Fig. 13, tsc) and projected anterolaterally, the projected parts inflected rather than flush with inner surface of mesoscutum (see discussion).





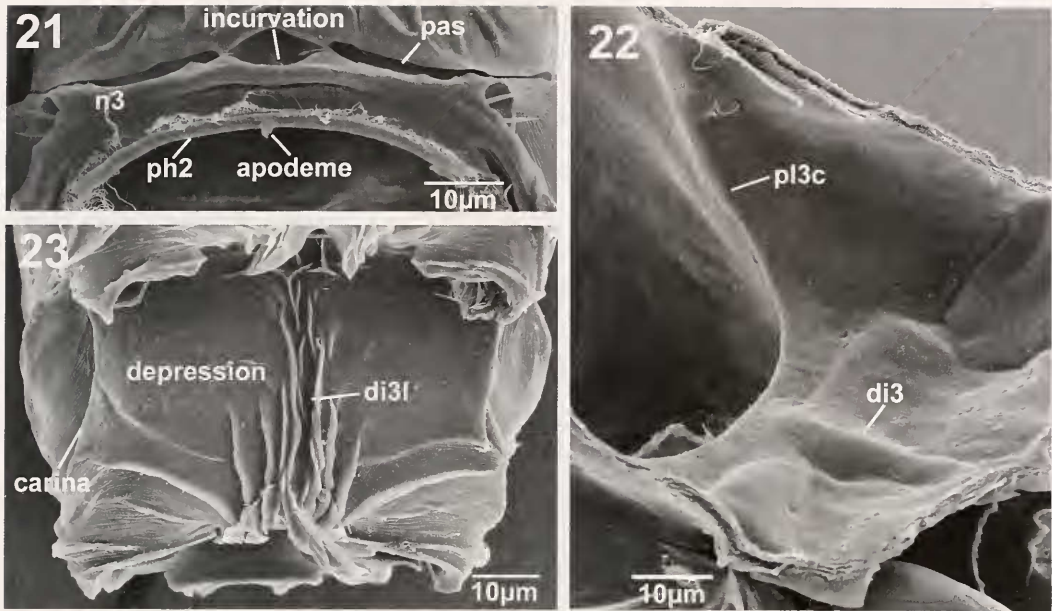
Figs 16–20. Mesopectus of *P. anomalum*. 16. Dorsal part of mesothorax, lateral view. 17. Ventral part of mesopleuron, ventral view. 18. Dorsal part of mesopleuron, internal view; 19. Posterior part of mesopleuron, posterior view. 20. Mesofurca, anterior view. Abbreviations: axc = axillar carina; cx2f = mesocoxal foramen; cx2ma = mesocoxal median articulation; di2 = mesodiscrimen; di2l = mesodiscriminal line; fu2a = mesofurcal arm; fu2p = mesofurcal pit; fw = forewing base; hw = hind wing; mpa = mesopleural arm; n1 = pronotum; ph2l = mesolaterophragmal lobe; pl3a = metapleural apodeme; psc = parascutal carina.

Mesophragma (Fig. 15) large, rectangular, extending far into propodeum almost to propodeal foramen; pseudophragmal lobes, ventral median longitudinal carina, and posterior median slit not developed, but with low, broad transverse swelling just posterior to anterior margin; anterior margin with tiny apodeme and associated

tendon medially (Fig. 21). Laterophragmal lobes developed as slender, ventromedially projected rods on anterolateral extensions of mesophragma (Fig. 18, ph2l).

*Mesopectus-metathorax-propodeum complex*.—Mesopectus in anterior view with mesopleural margins forming U-shape, lateroventrally with triangular flange op-

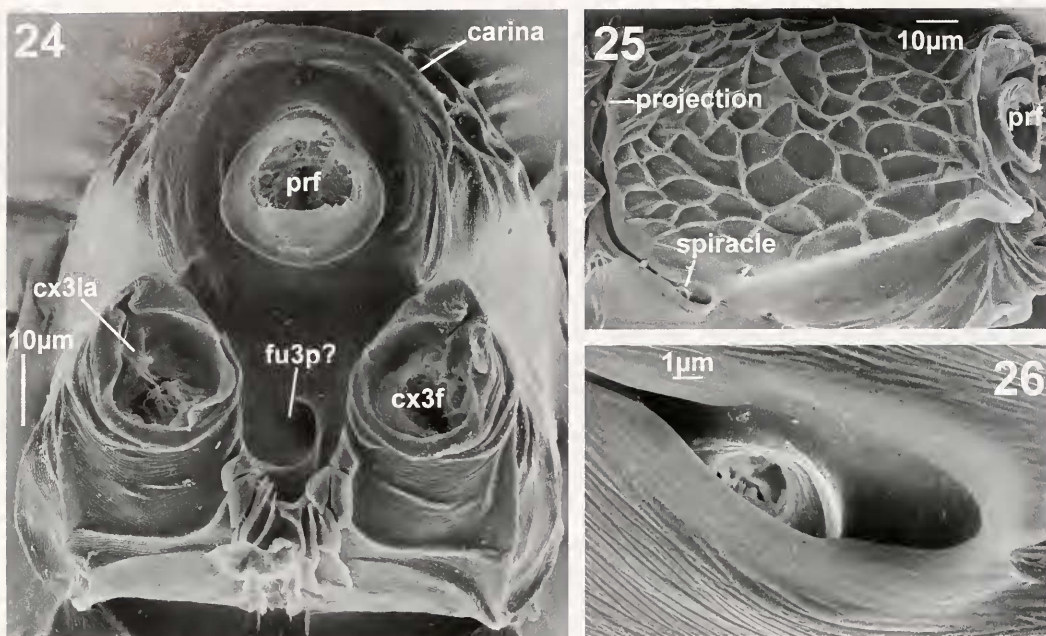




Figs 21–23. Metathorax of *P. anomalum*. 21. Metanotum, anterodorsal view (dissected from mesothorax). 22. Ventral metapleuron, internal view. 23. Ventral metapleuron, external view. Abbreviations: di3 = metadiscrimen; di3l = metadiscriminal line; n3 = metanotum; pas = propodeal antecostal sulcus; ph2 = mesophragma; pl3c = metapleural paracoxal carina.

posite basal part of procoxa, the flange laterally articulating with posteroventral corner of pronotum (Fig. 17, n1). Mesopleura with transverse sulcus extending along entire anterior margin, internally the sulcus corresponding to low transverse carina extending onto mesopleural arms (Fig. 18). Prospinasternum present as very small area anterior to transverse carina, hardly visible in external view; internally, prospinasternal apodeme absent (Fig. 9, sp1). Mesopleural arm (Fig. 16, mpa) dorsally accommodating fore wing articulation, posteriorly delimited by distinct notch; internally, mesopleural arm supported by short, almost vertical carina, ventrally delimited by short horizontal ledge connected to anterior transverse carina (Fig. 18). Mesobasalare and posterior thoracic (metathoracic) spiracle neither observed internally nor externally. Mesopleuron with lateral surface reticulate anteroventrally, smooth posterodorsally (Fig. 1); ventral surface reticulate/scaly,

with distinct spine anterolaterally (Fig. 17), and posteriorly with transverse carina delimiting smooth area around mesocoxal foramina (Figs 17, 19). Internally, mesopleural apodeme and mesepisternal ridge absent. Mesocoxal foramen (Fig. 19, cx2f) narrow, laterally overlapped by flange (Fig. 1) continuous with transverse carina; median mesocoxal articulation developed as short lobe (Fig. 17, cx2ma). Mesocoxa with proximal part (basicoxite) reduced. Mesodiscriminal line (Fig. 17, di2l) a longitudinal smooth groove extending from anterior margin of mesoplectus and terminating in mesopleural pit (Fig. 19, fu2p) between mesocoxal foramina. Internally, mesodiscrimen (Fig. 20, di2) anteriorly continuous with transverse carina; discrimen rising gradually to form high septum at point of origin of mesofurcal arms (Fig. 20, fu2a), then descending steeply to terminate in mesofurcal pit. Proximal part of mesofurcal arm slender, extending dorsolaterally, with shallow depression

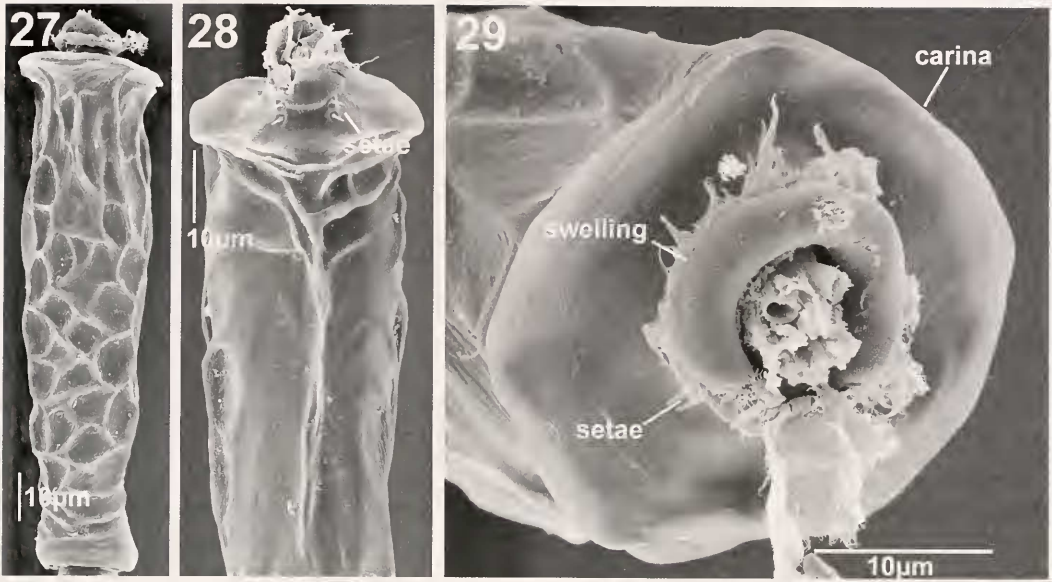


Figs 24–26. Propodeum of *P. anomalum*. 24. Posterior view; 25. Dorsolateral view; 26. Propodeal spiracle. Abbreviations: cx3f = metacoxal foramen; cx3la = metacoxal lateral articulation; fu3p? = possible metafurcal pit; prf = propodeal foramen.

dorsally; anterior mesofurcal apodemes, mesofurcal bridge, and mesospinasternal apodeme absent.

Metanotum (Figs 11, 21, n3) a narrow transverse strip between anterior margin of mesophragma and antecostal sulcus; without developed metascutellum but posteriorly with slight median incurvation delimited by minute posterior projections and laterally with depression having two short setae (Figs 11, 16, 21). Metapleuron broad dorsally, accommodating hind wing in incurvation in thickened dorsal margin (Figs 1, 16). Small, triangular projection posteriorly of hind wing separated from bulk of metapleuron by narrow sulcus (Figs 11, 16); projection with small bilobed, possibly membranous extensions posterodorsally. Metapleuron fused with mesopleuron for almost entire length laterally and ventrally (Fig. 1); separated from propodeum posterodorsally by antecostal suture (Fig. 1, pas), but fused with propodeum below propodeal spiracle, the boundary indicated by shallow groove

extending from metapleural pit to notch just dorsal to metacoxal foramen (Fig. 1). Metapleuron with lateral surface smooth except for striate sculpture just anterior of metacoxal foramina and with small pit in middle (Fig. 1, pl3p) continuous with shallow paracoxal sulcus extending ventrally (Fig. 1, pcs); internally, metapleural pit corresponding to low apodeme (Fig. 20, pl3a) situated at dorsal end of low paracoxal carina extending across ventral part of metapleuron (Fig. 22, pl3c). Metapleuron with ventral surface smooth except for low longitudinal ridge of scaly projections formed along metadiscal line (Fig. 23, di3l), the discal line extending to circular depression (Fig. 24, fu3p?) between metacoxal foramina. Internally, circular depression corresponding to slight swelling, and metadiscal line (Fig. 22, di3) developed as low longitudinal swelling reaching paracoxal carina; metafurca absent. Externally, metepisternal depression well developed laterally of metadiscal line, laterally delimited



Figs 27–29. First petiolar segment of *P. anomalum*. 27. Dorsal view. 28. Ventral view of anterior part. 29. Anterior view.

by low longitudinal carina (Fig. 23). Metacoxal foramen (Fig. 24, cx3f) constricted, circular, surrounded by raised rim, separated from propodeal foramen by cuticle; median metacoxal articulation not developed, lateral articulation (Fig. 24, cx3la) concealed in lateral view.

Propodeum dorsally with scaly-reticulate sculpture anterior to transverse, semi-circular carina above propodeal foramen (Figs 24, 25); bare except for long seta posterior to lateral end of antecostal suture (Fig. 1, pas); dorsally with minute submedian projection extending from anterior margin across antecostal suture to abut corresponding structure on metanotum (Fig. 25). Propodeal antecostal suture (Fig. 1, pas) a narrow transverse groove separating metanotum and propodeum (Figs 1, 21), the suture terminating laterally in small oval depression concealing propodeal spiracle (Figs 25, 26). Internally, propodeum with apodemes for spiracular muscles; metaphragma only observed laterally above propodeal spiracle, but median part might be indicated by presence of low transverse swelling anteriorly on me-

sophragma (Fig. 15; see above). Propodeal foramen (Fig. 24, prf) pear-shaped in outline, encircled by raised rim and surrounded by smooth cuticle; without distinct articulation process with metasoma.

*Mesosoma-metasoma articulation.*—Petiole two-segmented. First petiolar segment (predominantly abdominal T2, see discussion) slender, cylindrical, and dorsally reticulate (Fig. 27); anteriorly with portion articulating with propodeum constricted relative to rest of petiole (Figs 27, 28), its anterior margin swollen and circular in anterior view (Fig. 29); cuticle surrounding constricted portion smooth and posteriorly delimited by transverse carina encircling entire petiole (Figs 28, 29); anteroventrally with two sublateral setae on smooth surface posterior to anterior swollen margin (Figs 28, 29); with median longitudinal carina posterior to anterior transverse carina, but otherwise without conspicuous sculpture ventrally.

## DISCUSSION

Debauche (1948) confused the lateral parts of the pronotum in *P. anomalum* with



the propleuron, stating that 'les propleures atteignent, en arrière, les insertions alaires' [p. 31: 'the propleura reach the wing articulations posteriorly']. Gibson (1986) clarified the configuration of the pronotum and its association with surrounding sclerites. The condition in *P. anomalum* differs from Chalcidoidea in that the pronotum is rigidly associated with the mesopleuron, a large exposed prepectus is absent (therefore the posterodorsal corner of the pronotum and the fore wing base are not widely separated), and there is no exposed spiracle situated dorsally between the pronotum and the mesoscutum.

The above statements require some qualification. A more or less rigid association of the pronotum with the mesopleuron and concurrent absence of an independent prepectus is widespread within the Apocrita and has probably evolved independently a number of times (Gibson 1985, 1999). A number of taxa (Cynipoidea, Platygastroidea, most Proctotrupoidea) have the prepectus fused to the posterior margin of the pronotum as the posterolateral pronotal inflection, forming an articulation with the mesopleuron. This condition is apparently not present in *P. anomalum*. Gibson (1986) could not establish the identity of the prepectus in Mymarommatidae with certainty, but suggested it to be homologous with the narrow internal carina extending vertically close to the posterolateral margin of the pronotum. Our findings support this; the carina survived treatment with KOH and hence must be cuticular, and a sclerite in this position would be the prepectus by default. Furthermore, the carina is apparently continuous with the pronotum, there being no indication of displacement of the structure due to shrinkage of membranous cuticle (Fig. 4).

To further corroborate the identity of the prepectus, it would be desirable to establish the position of the anterior thoracic spiracle, which in most Hymenoptera is closely associated with the posterior mar-

gin of the pronotum anteriorly and the prepectus posteroventrally. An anterior thoracic ('mesothoracic') spiracle cannot be observed externally in *P. anomalum*. Gibson (1986) tentatively identified the spiracle in Mymarommatidae as a structure close to the posterolateral margin of the pronotum observed in a slide preparation, but was unable to confirm this with SEM investigations. Neither could we; the only internal structure observed close to the prepectus is a small pit just anterior to it (Fig. 4), and it likely is this pit that Gibson (1986) observed in the slide preparation. However, the pit is not associated with a tracheal trunk (unless the narrow tissue strands sometimes observed to issue from the pit are remains of this) or with an apodeme for a spiracle occludor muscle. The plesiomorphic condition in Hymenoptera is that the spiracle occludor muscle arises from the prepectus (Gibson 1985, Vilhelmsen 2000a). Consequently, *P. anomalum* apparently lacks a functional anterior thoracic spiracle.

Mymarommatidae also lacks a fore wing tegula according to Gibson (1986). Nevertheless, the condition in *P. anomalum* is not similar to that in most Chalcidoidea, in which there is broad contact between the mesoscutum and the exposed and dorsally expanded prepectus, which separates the tegula from the pronotum (a notable exception to this is the Rotoitidae, which have a slender, partially concealed prepectus; Gibson & Huber 2000). Even though the tegula is absent, the ventral part of the parascutal carina (Fig. 16, psc), which anteriorly delimits the concavity accommodating the tegula, extends anteriorly of the posterodorsal corner of the pronotum in *P. anomalum* (Fig. 16), like in virtually all Hymenoptera except Chalcidoidea, where the carina terminates well posteriorly of the corner. The configuration of the tegula and parascutal carina relative to the posterodorsal corner of the pronotum is correlated with the occurrence of a dorsally enlarged prepectus. In conclusion, the pres-

ence of a concealed prepectus not in contact with the mesoscutum in Mymarommatidae is plesiomorphic relative to Chalcidoidea, whereas the fusion of the prepectus to the pronotum is apomorphic, but paralleled in many other Apocrita (Gibson 1985, 1999). The absence of both tegulae and anterior thoracic spiracles are possibly autapomorphic for Mymarommatidae.

Another putative autapomorphy is the fusion of the medioventral margins of the propleura and the fusion of the prosternum to the propleura (Fig. 6). The boundary between the propleura and the prosternum is difficult to establish. The profurcal pit (Fig. 8, fu1p) is situated dorsally of the procoxal bases (Fig. 8, cx1); however, in most Hymenoptera the prosternum extends well ventrally of the pit before bending anteriorly above the propleura. We consider it most likely that the smooth areas medioventral to the procoxal bases are part of the prosternum (Fig. 8, st1) and the fusion with the propleura took place ventrally of these, just dorsally of the extended posteroventral margins of the propleura. Anteriorly, the boundary between the propleura and prosternum is even less obvious. The base of the profurca does not extend far anteriorly, indicating that the anterior part of the prosternum was short prior to fusion. However, those Chalcidoidea with an exposed, anteriorly extended prosternum also do not have the profurcal base extending far anteriorly (Vilhelmsen unpubl.; Krogmann unpubl.), so this feature is apparently of limited value in deducing the anterior limits of the prosternum.

In virtually all Chalcidoidea the medioventral margins of the propleura diverge posterolaterally to broadly expose an anteriorly extended, diamond-shaped prosternum (Krogmann 2005, Bucher 1948, fig. 18). In most other Hymenoptera, except for the basalmost lineages (Xyeloidea and Tenthredinoidea; Vilhelmsen 2000a), the medioventral margins abut for most of

their length from just posteriorly of the cervical prominences to the posterior margin of the propleura level with the procoxal bases, and cover the anteroventral part of the prosternum if the latter is developed. Given that the Mymarommatoida is the putative sistergroup of Chalcidoidea, it would be highly informative to know what the configuration of the prosternum was prior to its fusion with the propleura. Because of the difficulties with establishing the anterior boundary of the prosternum in *P. anomalum* (see above) it is not possible to determine this condition.

The fusion of the propleural and profurcal arms in *P. anomalum* (Fig. 9) is another putative mymarommatid autapomorphy and possibly correlated with the fusion of the prosternum and propleura. In other Hymenoptera, the lateral end of the profurcal arm articulates with the posterodorsal margin of the propleuron, an autapomorphy of the Hymenoptera (Vilhelmsen 2000a). The propleural-profurcal articulation perhaps forms a suspension for the fore legs. The fore legs articulate with the propleura and abut the prosternum. The propleural-profurcal articulation presumably allows the prosternum to become slightly displaced relative to the propleura, thus softening the impact of the legs on the substrate and dampening it before it is transmitted to the head. The fusion of the propleura and the prosternum in *P. anomalum* could have made the articulation redundant because the prosternum and propleura are immovable relative to one another. The profurcal bridge, a sclerotised connection between the opposite dorsal parts of the profurcal arms extending above the ventral nerve cord, is also missing from the majority of Chalcidoidea (Krogmann 2005). However, the occurrence of this feature is highly variable throughout the Apocrita (Vilhelmsen 2000a, unpublished observations).

The exposed cervical prominence at the anterolateral corner of the propleuron (Fig. 7, cep) is a feature shared by *P.*

*anomalum* and at least some Chalcidoidea (unpublished observations). In most other Apocrita, the cervical prominence is somewhat retracted and below the anterodorsal corner of the propleuron (Vilhelmsen 2000a). The condition in *P. anomalum* is perhaps correlated with miniaturization. The small number of sensilla (3) at the cervical prominence probably also is a consequence of small size; other, larger Hymenoptera, have up to 20–30 sensilla in this position on a prominent cervical swelling (Vilhelmsen 2000a, unpublished observations).

In *P. anomalum*, the dorsal posterolateral corner of the propleuron accommodates the posteroventral corner of the pronotum in a distinct groove (Figs 2, 8). This is not observed in any Chalcidoidea, where the pronotum is much less integrated with adjacent sclerites (see above). A similar condition to that in *P. anomalum* is possessed by most Ichneumonoidea (unpublished observations). No other features appear to link Ichneumonoidea with Mymaromatidae, so the condition in *P. anomalum* is probably independently derived and a further putative autapomorphy of Mymaromatidae.

The prothorax of *P. anomalum* differs from that of Chalcidoidea in not being subdivided medially by a slit and not extending laterally. The presence of a slit and the absence of a lateral extension of the prothorax are the plesiomorphic conditions, being common within Hymenoptera. Furthermore, the prothorax has rods extending from it dorsally (Fig. 14), which have not been observed in any other Hymenoptera. The function of these rods could not be ascertained, but it is likely they are apodemes that accommodate prothorax-pronotal muscles; indeed, what appears to be tonofibrillae were in some instances associated with the rods (Fig. 14, tf). The position and configuration of the prothorax rods might indicate that they are serial homologues of the axillar phragmata (see below), which arise just anteriorly of the mesothorax. Unlike

the axillar phragmata, the prothorax rods probably do not accommodate nototrochanteral muscles because pronoto/phragmal-protrochanteral muscles are absent from the Hymenoptera that have been examined for musculature, although pronotal-procoxal muscles do occur (Vilhelmsen 2000a). The presence of axillar phragmata remains the most convincing synapomorphy for Chalcidoidea and Mymaromatidae (Gibson et al. 1999). The homology of the structures in the two taxa is based on the topology regarding muscle attachments and position relative to the surrounding structures. However, the configuration of the axillar phragmata is quite different from that of Chalcidoidea. In Chalcidoidea, the phragmata are flat, broad structures that usually lie adjacent to the internal part of the mesoscutum (Krogmann 2005). In *P. anomalum*, the phragmata are slender, cylindrical rods that are continuous medially through the transscutal carina (Fig. 13, tsc) and project away from the mesoscutum into the lumen of the mesosoma. The difference in structure and the possibility that in Mymaromatidae the axillar phragmata are serial homologues of the prothorax rods, might indicate that they were independently derived from those of Chalcidoidea. Alternatively, the difference in structure of the axillar phragmata between Mymaromatidae and Chalcidoidea may reflect simple size differences in the tergo-trochanteral muscles or some other functional requirement.

The mesoscutum anteriorly of the transscutal articulation in *P. anomalum* is devoid of any external and internal features (mesoscutal sulcus, notauli, parapsides). Most apocritan wasps, including Chalcidoidea, have at least the notauli developed. The posterior border of the axilla in *P. anomalum* is delimited internally by the posterior margin of the axillar phragmata and the lateral mesoscutellar carina.

The transverse subdivision of the mesoscutellum into an anterior raised part



and a posterior depressed part (further emphasized by the difference in sculpture in *P. anomalum*, Figs 10, 11) is also observed in some Chalcidoidea (Krogmann 2005). In the Chalcidoidea, the posterior part is known as the frenum, and the dividing line as the frenal line. If the presence of a frenum is a ground plan feature of the Chalcidoidea, it might be an additional putative synapomorphy of Mymarommatidae and Chalcidoidea (Gibson et al. 1999). The identity of the frenum in Mymarommatoidea is corroborated by its relation to the mesoscutellar arms, the latter arising just anteriorly of the external frenal line (Fig. 10, frle) as in those Chalcidoidea having a frenum. Of the two branches of the axillar carina in *P. anomalum*, the anterior is probably homologous with the single carina in most other Hymenoptera, because it terminates at the anterior end of the mesoscutellar arm, the normal condition in taxa with only one branch.

The large, rectangular mesophragma with a straight posterior margin extending through most of the propodeum in *P. anomalum* is a feature also observed in some Mymaridae (e.g., *Gonatocerus*; unpublished observations). If Mymaridae are indeed basal within the Chalcidoidea (Gibson et al. 1999), this configuration of the mesophragma is putatively the ground plan condition for Chalcidoidea. Many Chalcidoidea have the mesophragma tapered posteriorly and with an incurvation in the posterior margin (e.g., Bucher figs 28–29), as do most Hymenoptera. The muscle arising from the apodeme medially on the anterior margin of the mesophragma (Fig. 21) is probably homologous with the mesoscutellar-metanotal muscle arising from the anterior margin of the metanotum in other Hymenoptera. Heraty et al. (1994) did not detail the condition in Mymarommatidae or report a similar configuration for any other taxa they examined; the muscle also inserts on the anterior margin of the mesophragma

in *Xiphydria* (Xiphydriidae; Vilhelmsen 2000b).

The extensive fusion in the mesosoma forming the mesopectus-metathorax-propodeum complex is not unique for Mymarommatidae. Indeed, the fusion between the propodeum and posterodorsal part of the metapleuron is an autapomorphy for the Apocrita (Vilhelmsen 2000b). Within the Apocrita several taxa have the meso- and metapleura fused to varying degrees, but only in Mymarommatidae and Ceraphronoidea are they fused along almost their entire common boundary (Vilhelmsen unpublished). The integration in Ceraphronoidea has gone even further, because the dorsal and ventral parts of the metathorax have become almost entirely reduced. In Chalcidoidea, the meso- and metapleura closely abut, as in all Apocrita, but usually are not fused.

The pronounced integration and general scarcity of anatomical reference points in the mesopectus-metathorax-propodeum complex means that the boundaries between the constituent parts can only be loosely established. The following anatomical features are relevant for this exercise: the fore and hind wing bases, the lateral ends of the metathorax, the metapleural pit, the propodeal antecosta and spiracle, the meso- and metacoxal cavities and lateral articulations, the meso- and meta-furcal pits, and the propodeal foramen.

The lateral boundaries between the meso- and metapleuron and the propodeum are indicated in Fig. 1. The dorsal endpoint of the boundary between the meso- and metapleuron can be identified at the bottom of the slit that separates the fore- and hind wing bases (Fig. 16). The posterior thoracic spiracle would have provided a useful landmark, but is apparently absent, as in many apocritan wasps, including Chalcidoidea (unpublished observations). Posteroventrally, the boundary between the meso- and metapleuron probably lies just anteriorly of the metapleural paracoxal sulcus, which extends as a verti-

cal groove from the metapleural pit to the notch above the mesocoxal foramen (Fig. 1). Ventrally, the boundary between the two regions is more easily identified by the groove that extends between the notches above the mesocoxal foramina and the mesofurcal pit (Figs 19, 23). The mesofurcal pit lies between the coxal foramina, not anteriorly of them as in almost all Chalcidoidea; the anterior position of the mesofurcal pit is a putative autapomorphy of the Chalcidoidea. A transverse carina is present just anteriorly of the mesocoxal foramina and pit as in Chalcidoidea, but also in some other Apocrita.

The mesofurca in *P. anomalum* is comparatively simple, lacking a mesofurcal bridge or any conspicuous apodemes (Fig. 20). The mesofurcal bridge is also absent from some Chalcidoidea, notably putatively basal taxa such as Mymaridae and Rotoitidae. This was noted by Heraty et al. (1997), but because of its widespread occurrence in Apocrita they considered the presence of a bridge to be the ground plan state for Chalcidoidea. The proximal part of the mesofurcal arm is only slightly depressed in *P. anomalum*. In most Chalcidoidea, a distinct dorsal concavity is developed to various extents in this region, a putative autapomorphy for the superfamily.

The boundary between the metathorax and propodeum is comparatively easy to establish, at least dorsally, being marked by the antecostal suture (Fig. 1). The putative boundary then extends between the lateral end of the suture and the metapleural pit towards the metacoxal lateral articulation along a shallow groove (Fig. 1). Posteriorly, the boundary extends between the metacoxal and propodeal foramina (Fig. 24). Apparently, the lateral part of the metapleuron is expanded dorsally and ventrally, but constricted near the metapleural pit (Fig. 1).

The metanotum is reduced in comparison to most other Hymenoptera, but is still

identifiable. No distinct features (e.g., metascutellum) are evident (Figs 11, 21) other than the two small submedian projections that extends across the antecostal suture to abut similar, anteriorly projecting structures on the propodeum. Such structures are absent from Chalcidoidea (unpublished observations), but they might be homologous with those observed in many Proctotrupoidea, Cynipoidea, and Ichneumonoidea.

The function of the triangular projection posteriorly of the hind wing and the bilobed extensions it accommodates (Figs 11, 16) is unknown; the extensions may possibly serve as sensillae monitoring the movements of the hind wing base. It is also unclear whether the extensions are membranous; if they are, their bilobed configuration is possibly an artifact.

Internally, the metapleuron has a low internal swelling (Fig. 20, pl3a) that corresponds to the metapleural pit (Fig. 1, pl3p) and which is apparently the reduced metapleural apodeme. The low carina extending between the apodemes is the paracoxal carina, usually situated along the anterior margin of the metapleura (Fig. 22, pl3c); this configuration of the apodeme and carina is widespread in Apocrita. The metafurca is usually closely associated with the paracoxal carina, the metafurcal arms arising medially at the anterior end of the metafurcal discrimen (Vilhelmsen 2000b). In *P. anomalum*, the only remnant of the metafurca is the median depression between the metacoxal foramina (Fig. 24, fu3p?), which probably corresponds to the metafurcal pit, and a low longitudinal swelling (Fig. 22, di3) that corresponds to the metafurcal discrimen. The entire absence of metafurcal arms is a putative autapomorphy for the Mymarommatidae. In Chalcidoidea, there is substantial variation in the configuration of the metafurcal arms and the number and configuration of the metafurcal pits (Krogmann 2005). Unfortunately, the absence of the former structure in Mymar-

ommatidae makes it difficult to interpret the evolution of this structure within Chalcidoidea.

The accommodation of the propodeal spiracle within the lateral ends of the antecostal suture (Fig. 26) is also observed in *Trichogramma* (Krogmann 2005), but not outside Chalcidoidea. A more comprehensive survey of the occurrence of this trait within Chalcidoidea is required to establish its possible phylogenetic significance. The presence of well developed apodemes internally of the spiracle indicates that it is the only functional spiracle in the mesosoma of *P. anomalum*.

The slender, two-segmented petiole is only observed in the extinct taxon Serphitidae apart from in Mymarommatidae; based on this, it has been hypothesized that they form a monophylum (cf. Gibson 1986). The first petiolar segment of *P. anomalum* essentially is a narrow, sclerotised tube with little indication of boundaries between individual sclerites. This condition occurs in many Apocrita, including some Chalcidoidea, and is difficult to interpret. The ventral longitudinal carina extending along most of the first petiolar segment in *P. anomalum* is perhaps formed by the fusion of the lateral margins of the second abdominal tergum (T2), indicating that T2 is expanded ventrally and the sternum of this segment is reduced or absent (Gibson in litt.). However, the setae situated anteroventrally just posterior to the anterior margin of the first petiolar segment (Figs 28, 29) are probably homologous with the sensillar patches situated sublaterally on S2 in Apocrita that have this sclerite separate from T2. This indicates that at least the anteriormost part of S2 is present in *P. anomalum*. The continuous transverse carina anteriorly on the first petiolar segment (Fig. 29) is also observed in many Proctotrupoidea, Cynipoidea, Platygastridae, Ceraphronoidea as well as in some Chalcidoidea (unpublished observations).

## CONCLUDING REMARKS

The present study underlines the highly autapomorphic status of the Mymarommatidae. However, we have only examined *P. anomalum*, and the features we have studied need to be surveyed for a larger sample of the family. According to Gibson et al. (1999), the diversity of Mymarommatidae is not sufficiently reflected by the current classification that has all extant species lumped in *Palaeomymar*, a situation that will probably change once the family has been comprehensively revised. Given the small size of all Mymarommatidae and that it possibly occupies a key phylogenetic position within Apocrita, detailed morphological studies of additional species are recommended to test our inferences.

Many of the putative autapomorphies of Mymarommatidae are reductional and probably correlated with miniaturization (e.g., the absence of the anterior thoracic spiracle and the metafurca). Furthermore, being morphologically highly derived and isolated confounds attempts to homologize features with those in other Apocrita (e.g., the extensive fusion in the propectus, the difficulties in establishing the identity and configuration of the propectus). The sistergroup relationship to the Chalcidoidea (also a highly autapomorphic taxon) seems the best supported hypothesis at present, but may prove difficult to corroborate further from morphological evidence alone. Mymarommatidae has not been represented in any phylogenetic analyses of Hymenoptera including molecular data, not even the most recent comprehensive ones (Campbell et al. 2000, Dowton and Austin 2001). Sequence data might confirm or challenge current concepts of the phylogenetic affinity of these intriguing animals.

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